Aquatic Distributional Patterns in the Interior Low Plateau

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ABSTRACT.— The aquatic gastropod and fish faunas of the Interior Low Plateau of extreme southern Indiana, Illinois (Wabash River drainage), Kentucky, Tennessee, and northern Alabama reflect the interaction of tectonic changes, glaciation, eustatic stream modifications, piracy within the Low Plateau and in extralimital drainages (particularly the Coosa-Alabama system), immigration from trans-Mississippian systems, speciation within drainages that cross the Low Plateau, and survivorship as relicts. Examples in the Pleuroceridae, Unionidae, and several fish families are discussed, with emphasis on percid darters and the catfish genus *Noturus*.

INTRODUCTION

The Interior Low Plateau of extreme southern Indiana, Illinois (Wabash River drainage), Kentucky, Tennessee, and northern Alabama (Fenneman 1938; Quarterman and Powell 1978) is a biological crossroads between regions that are faunistically and floristically rich. Understanding of the biological importance of this unique region has come very slowly, piecemeal really, mostly because of inadequate study and failure in the synthesis of existing information. The present biota is quite complex, consisting of mixtures of types from diverse centers of origin, including a rather large number of relicts and endemics. To extrapolate from knowledge of existing biotas back into the past in order to understand the present is not a bad approach, particularly if there are considerable supporting geologic and paleontologic data available.

MOLLUSCA

In the discussion that follows, I have elected to retain Goodrich's nomenclature (see literature cited) rather than the combinations recently espoused by Burch (1982), since most readers are not familiar with the resurrected combinations. Furthermore, there is still considerable disagreement regarding some of the combinations.

In the early part of this century, well-diggers near Henderson, Kentucky, cut into a deposit 25.5 m below the surface. The strata were determined to be of Yarmouthian Interglacial age (Baker 1920). The mollusks removed from those deposits included specimens of *Campeloma crassula* Rafinesque, *Pleurocera canaliculatum* (Say), *Planorbula*

(*Menetus*) *dilatatus* (Gould), and *Valvata* species. The Yarmouthian followed the Kansan glacial epoch and was the longest interglacial. During that period the climate was slightly warmer than at present (Fenneman 1938), allowing many species to extend their ranges (Baker 1920). Later investigations of Yarmouthian deposits near Evansville, Indiana (Baker 1920), disclosed the presence of unionid clams and various snails that no longer live in streams of the Interior Low Plateau. For example, *Quadrula quadrula asper* (Lea 1831) now lives in streams that drain into the Gulf of Mexico from Alabama to central Texas and northward to Kansas. Another species with derivatives still present in many Low Plateau streams, *Amblema plicata* Say, has its principal and parental stocks distributed from the Alabama River drainage and streams flowing into the Gulf of Mexico west to central Texas and north to central Kansas. Three additonal operculated snails were found in the well deposits: *Pleurocera unciale* (Haldeman), *P. alveare* (Conrad), and a species of *Lioplax*. The last two still live in the Ohio River and many of its tributaries, whereas the first is now restricted to the upper tributaries of the Tennessee River in Virginia and eastern Tennessee (Burch 1982; Goodrich 1940); all have their principal relatives in the Alabama River system.

Many deposits of the previous Aftonian Interglacial and the Illinoian glacial period (Browne and Bruder 1963) indicate climatic conditions that were considerably cooler and moister than at present. Ice movement, completely overwhelming stream systems to the north, caused a southward shift of faunas and, upon recession, a re-expansion northward. Thus, many of the species found themselves exposed to new environmental and competitive conditions that perhaps stimulated extensive differentiation into species and races in extralimital areas. Many gastropod species that are now restricted to more northerly latitudes occurred in the Interior Low Plateau during Pleistocene times (Browne and Bruder 1963) although some derivative species remain. They include *Amnicola*, various species of *Lymnaea*, and *Helisoma anceps* (Menke) (Branson 1972).

The presence of the Alabama and Tennessee river system derivatives in Interior Low Plateau streams, as far north as the Wabash River of Indiana and Illinois, raises questions regarding migratory pathways and strengthens a theory previously in vogue. Baker (1920) postulated existence of an Appalachian river that included parts of the old Teays and Tennessee rivers and their tributaries above Chattanooga and the Coosa-Alabama system. Whether it is necessary to invoke the existence of such a river is open to debate; other mechanisms can explain the observed distributions. However, that the Alabama River system, in particular the Coosa basin, has been a potent generator of species is scarcely open to argument. The Coosa River had more endemic species of operculated gastropods than any other river in North America (Goodrich 1944a), including members of the families Pleuroceridae and Viviparidae. Two of eleven species of *Somatogyrus* that occur in the Coosa also live in the Tennessee River, and *Goniobasis carinifera* (Lamarck) lives in both drainages (Goodrich 1944a).

A very characteristic pleurocerid genus of the Alabama-Coosa system is *Anculosa* (*Leptoxis*, according to Burch 1982), which has a large number of endemic species not found outside that system but also has derivatives that occur elsewhere (Goodrich 1922). Some of these species occur in Low Plateau drainages, including the related genus *Nitocris* (Branson 1972). *Nitocris* (relegated to *Mudalia* by Burch 1982) has been able to extend its range into the Kanawha of West Virginia, the Hiwassee of North Carolina, the Tennessee River, and the Ohio and Little Miami of Ohio, Indiana and Kentucky (Goodrich 1940, 1944a). Alabama River derivatives of *Anculosa* occur in the Tennessee, Cumberland and Green rivers (Burch 1982; Goodrich 1934). *Anculosa subglobosa* Say lives in the Cumberland River system of central Tennessee (Goodrich 1921). *Anculosa praerosa* Say, a secondary Tennessee River system derivation, occurs in the Tennessee system; in the Cumberland, Holston, Duck, Clinch, Little Tennessee, and Obey rivers of Tennessee; in tributaries of the Duck and Tennessee rivers in Alabama (Burch 1982; Goodrich 1944b; TVA 1975); and in the Blue and Wabash rivers of Indiana. Thus, it is clear that streams of the Interior Low Plateau have served as important migration pathways into the Ridge and Valley Province and elsewhere.

There are many endemic pleurocerid species in the Tennessee and Cumberland river systems (Goodrich 1940). *Pleurocera prasinatum* (Conrad) of the Alabama River system is most closely related to *P. canaliculatum* (Say) (Goodrich 1935), various forms of which occur in the Tennessee, Cumberland, Clinch, Kentucky and Ohio rivers. It has also been able to penetrate into the Wabash of Indiana (Goodrich 1929), doubtless via the Ohio since the ancestral Wabash of Indiana and Illinois was almost completely overwhelmed during Wisconsin glaciation. *Lithasia obovata* (Say) and *L. geniculata* Haldeman are both considered Tennessee River derivatives. *Lithasia geniculata* is relatively widespread in the Interior Low Plateau of the Tennessee River in Tennessee (Burch 1982). It was recently discovered in the southwestern section of the Kentucky portion of the Low Plateau (Branson et al. 1983), and is common in parts of the lower Tennesse (TVA 1975). *Lithasia obovata* had spread from the Tennessee River basin into the Green, Cumberland and Kentucky river basins and, via the Ohio River, into the Wabash of Indiana and the Scioto of Ohio (Goodrich 1929).

Goniobasis laqueata (Say), common in the Tennessee River basin (TVA 1975) and Cumberland River (Branson and Batch 1982), is another species that has spread into various segments of the Interior Low Plateau drainages from the Tennessee basin. *Goniobasis semicarinata* has its center of distribution in the Kentucky River drainage (Branson and Batch 1981). It entered the Cumberland River (Branson and Batch 1982), possibly by stream capture such as that documented by Kuehne and Bailey (1961), and the Salt River of Kentucky and the Wabash of Indiana (Goodrich 1935), perhaps by tributary hopping and reinvasion.

Many additional examples in the Pleuroceridae and Unionidae illustrate the principles involved, but the ones presented here shall suffice. From the very rich centers of endemicity in the Alabama-Coosa system and secondary speciation centers in the Tennessee and Middle Cumberland systems, the Pleuroceridae and Viviparidae (*Somatogyrus*, *Viviparus*, *Campeloma*) expanded northward and westward into the Cumberland, Green and Lower Tennessee rivers, and via them into the Ohio River basin. Depauperacy is one of the main features in the northern part of the area. The Tennessee and Cumberland rivers served as major refugia for unionid species that later reinvaded upstream Ohioan streams, and the Green River may have served as a refugium as well. All three rivers were sources for repopulation of the Wabash and Maumee rivers in postglacial times (Johnson 1980). Pleurocerids were able to reinvade Ohio and Indiana from similar sources via the Ohio River, penetrating into the Wabash River and its tributaries. Or perhaps, as discussed below, they came from some of the other old tributaries of the Teays system.

FISHES

Fish and mollusk distributional patterns in the Interior Low Plateau must be correlated with various physical and hydrologic phenomena in order to account for observed faunal relationships between drainage basins. According to Lachner and Jenkins (1971), there are four principal ways that aquatic organisms have achieved or may achieve new dispersal distributions: (a) stream capture, (b) eustatic changes in coastal plains, (c) Pleistocene modifications of drainages, and (d) movements from one drainage to another via past and existing interconnecting main streams. These mechanisms were perhaps involved in structuring the fauna of the Interior Low Plateau. Pleistocene glaciation certainly affected the region, very obviously so in the Shawnee Hills, the northern boundary of which (38th parallel) is demarked by glacial till (Harker et al. 1980, and literature cited therein). In this same general area, numerous karsts and faults crisscross the Green, Pond, Tradewater, Rough, Barren, and Ohio rivers.

To the west and southwest the Plateau is separated from the Coastal Plain Province by the Tennessee and Cumberland rivers in Kentucky, except along a narrow isthmus that abuts Missouri after crossing extreme southern Illinois, and by the Tennessee River in Tennessee and northwestern Alabama. The whole plateau is an ecotonal region, past and present, that lies in the western mesophytic forests, although slender extensions of the southeastern forests penetrate along rivers. The narrow connection between the Ozark Plateau and the Low Plateau through Indiana and Illinois has exerted an important influence on the floras and faunas, both east and west (Conant 1960).

In postglacial times, particularly during the so-called Climatic Optimum, the mesic forest and its streams, many of which are now buried (Wayne 1952), were apparently much more extensive than at present. They extended well up into the glaciated parts of Ohio, Indiana and Illinois. During the Xerothermic period that followed, the mesic forest vanished from most of the area above the Ohio River (Conant 1960), forcing a shrinkage in ranges of many organisms and leaving many of them in the narrow isthmus, an area thought to have been stable along the upper margin of the Mississippian Embayment since at least Tertiary times. Conant (1960) believed that many organisms used this narrow isthmus to extend their ranges east and west, including various species of *Eurycea*, *Plethodon*, and *Natrix*, and the fishes *Hybopsis dissimilis* (Kirtland), *Noturus eleutherus* (Jordan), and *Notropis galacturus* (Cope). *Etheostoma microperca* Jordan and Gilbert, certain species of the percid subgenus *Nothonotus*, and *Notropis telescopus* (Cope) may have been involved in such exchanges as well. However, Pflieger (1971) noted that the hill country around the head of the Mississippi Embayment may have played a role in various eustatic changes that allowed fish exchanges through the Embayment rather than around it via streams now absent.

Older geologic changes doubtless played a role in determining various aspects of the Interior Low Plateau's fauna, particularly pre-Cretaceous and Cretaceous Appalachian peneplanation (Griswold 1895, and others). One portion of such peneplains has been mapped westward through the Mississippi Embayment into Arkansas and northern Alabama, an important fact considering the putative sources of many Low Plateau organisms. Not only is the ancestral Cumberland River supposed to have crossed the northwestern Alabama axis, but there is a possibility that a Lower Mississippi stream, working backward from the embayment, captured much of the interior drainage from the old Teays system (Griswold 1895), transferring many aquatic species with it. Later events would have been of greater importance.

The Teays and the Old Ohio rivers greatly influenced the distribution of fishes and other aquatic organisms in the Low Plateau. According to Hocutt (1979), the Old Ohio River headed near the present confluences of the Salt River (Kentucky) and the Blue River (Indiana), a major tributary being the Green River from Tennessee and Kentucky. The Teays headed in North Carolina and flowed through Ohio, Indiana, and Illinois, then southward into the Mississippi Embayment; its major southern tributaries were the Old Kentucky and Old Licking rivers (Hocutt et al. 1978). Pleistocene glaciation destroyed most of the Lower Teays, creating the vast Upper Ohio River by westward diversion of the Big Sandy, Little Sandy, Licking, Kentucky, and Kanawha rivers and, during Kansan times (Wayne 1952), by diverting a large segment of the Teays system into the Wabash River. Such drainage modifications allowed eastern fishes, such as *Percina macrocephala* (Cope) and *Etheostoma blennioides blennioides* Rafinesque, to disperse westward into Low Plateau streams. This may account for the strong resemblances between the fish faunas of the Green and Licking rivers (Retzer et al. 1983) and the distribution of *Percina cymatotaenia* (Gilbert and Meek) and its undescribed sibling species (Branson and Batch 1974).

Lachner and Jenkins (1971) considered the Teays River to have functioned as a generation center, a reservoir of species, and a dispersal pathway. According to them, for example, the ancestral stock of *Nocomis micropogon* (Cope) evolved in the Upper Teays (Kanawha-New) system, and dispersed from there into the Lower Teays and into the southwestern Ohio basin. Since the Wabash was nearly completely overwhelmed by Pleistocene ice, the population in that stream has to be the result of later re-invasion from refugia to the south. Lachner and Jenkins (1971) presented evidence that *N. micropogon* entered the Tennessee River via stream capture, probably by headwater piracies between the Tennessee, Chattahoochee and Savannah rivers (Ross 1971). Ross (1971) also documented transfers of the Duck and Elk rivers from the Cumberland to the Tennessee and stream captures between the Coosa-Hiwassee and Tennessee rivers in northern Alabama. A Cumberland-Kentucky river drainage exchange of *Etheostoma sagitta* (Jordan and Swain), and doubtless other fishes as well, including *N. micropogon* (the only *Nocomis* in most of the Kentucky River), was documented by Kuehne and Baily (1961). If true, these exchanges would explain many of the mollusk and fish distributional patterns mentioned previously and below, and would strengthen the idea that the Tennessee, Coosa-Alabama , and Cumberland rivers have been potent differentiation and dispersal centers for various piscine, molluscan, and other groups of aquatic organisms.

There appears to have been considerable faunal exchange between the Alabama River system and the Mobile basin and the Tennessee River. The Tennessee and Alabama river systems share many species of fishes (Table 1), and the Mobile and Escambia drainages share at least seven species: *Hybognathus hayi* Jordan, *Pimephales notatus* (Rafinesque), *Notropis baileyi* Suttkus and Raney, *Etheostoma histrio* Jordan and Gilbert, *E. proeliare* (Hay), *Percina ouachitae* (Jordan and Gilbert) (=*P. uranidea* (Jordan and Gilbert)), and *Stizostedion vitreum* (Mitchill) (Lee et al. 1980; Smith-Vaniz 1968). Many of these species, of course, range over much of the Low Plateau, although some of them are more restricted in distribution and some species have been unable to effect exchange between the river systems. *Etheostoma squamiceps* Jordan, for example, occurs in southern Illinois, western Kentucky, and southwestern Indiana (Wabash drainage in Posey County), and in the Tennessee River system of west-cental Tennessee, Alabama, and Mississippi (Page et al. 1976), but has not been reported from the Alabama River system. Many *Nothonotus* and *Catonotus* show similar distributional patterns, albeit superimposed upon strong endemicity.

The Tennessee, Cumberland and Green river systems have received varying contributions to their fish faunas from other systems, and have made contributions to other drainages in the Interior Low Plateau. All have served as piscine speciation centers and as reservoirs for endemic species. One of the sources for Low Plateau fishes was obviously the Lower Mississippi River system, but the species derived from there mostly exhibit marginal or extralimital patterns in the Plateau. Exceptions are seen in the Green and Tradewater rivers, Kentucky, where they have effected rather wide distribution. Elsewhere, these fishes retain populations in more or less stable, protected, relict habitats, like those reported by Gunning and Lewis (1955) in southwestern Illinois. The species assemblage of that swampine environment includes fishes with mostly southern affinities: *Aphredoderus sayanus* (Gilliams), common in the Green River; *Umbra limi* (Kirtland); *Fundulus notti* (Agassiz); *Elassoma zonatum* Jordan, historically common in both the Green and Tradewater rivers; *Lepomis symmetricus* Forbes; *Centrarchus macropterus* (Lacépède), common in the Green River; *Etheostoma gracile* (Girard), common in the Green River; and *Chologaster agassizi* Putnam, not southern but Low Plateau. *Umbra limi*, which also occurs sporadically along the margin of the Low Plateau (Clay 1975; Sisk 1973), is of northern origin. According to Wiley (1977), the *Fundulus notti* species complex originated in the Lower Mississippi basin and, abetted by stream captures between the Mississippi and the Mobile Bay drainages, spread elsewhere. *Fundulus notti* barely penetrates southwestern Kentucky (Burr 1980) and Tennessee (Baker 1939) outside the Low Plateau. In Tennessee, the only non-embayment record for *F. notti* is from the Big Sandy River, a system with a host of embayment species, although the species is widespread in the Obion, Forked Deer and Hatchie rivers (D. Etnier, pers. comm.).

A large percentage of the fishes in southern Indiana and adjacent Illinois and Kentucky are of southern or lowland origin, many of them doubtless gaining entry in post-glacial times by migration through the Ohio River and its tributaries. Illinois, for example, has two species complexes that are coincidental with the Mississippi and Ohio river drainages, respectively (Forbes 1909; Smith 1979), entering the area via the Wabash and smaller Ohio River tributaries. Included in this list are: *Ichthyomyzon bdellium* (Jordan), *Lampetra aepyptera* (Abbott), *Notropis atherinoides* Rafinesque, *N. fumeus* Evermann, *N. shumardi* (Girard), *N. venustus* (Girard), *N. volucellus* (Cope), *Ericymba buccata* Cope, *Nocomis micropogon* (Cope), *Hybopsis amblops* (Rafinesque), *H. gracilis* (Richardson), *H. meeki* Jordan and Evermann, *Noturus flavus* Rafinesque, *N. miurus* Jordan, *N. eleutherus* Jordan, *N. stigmosus* Taylor, *Fundulus olivaceus* (Storer), *Aphredoderus sayanus* (Gilliams), *Lepomis megalotis* (Rafinesque), *Centrarchus macropterus* (Lacépède), *Micropterus punctulatus* (Rafinesque), *Elassoma zonatum* Jordan, *Ammocrypta pellucida* (Putnam), *Percina ouachitae* (Jordan and Gilbert), *Etheostoma blennioides* Rafinesque, *E. fusiforme* (Girard), *E. histrio* (Jordan and Gilbert), *E. kennicotti* (Putnam), *E. proeliare* (Hay), and *E. squamiceps* Jordan. Properly speaking, *Etheostoma proeliare* is a fish of the Coastal Plains and Mississippi Embayment (Burr and Page 1978), as is *E. fusiforme* (Sisk 1973), and the distributional center of the subgenus *Ammocrypta* appears to have been in the Lower Mississippi basin (Williams 1975). In the Low Plateau region, *A. pellucida* is the most widespread member, but *A. clara* Jordan and Meek is known from the Green River in Kentucky. *Fundulus chrysotus* (Günther), *Notropis maculatus* (Hay), and *Menidia beryllina* (Cope) are all distinctive Gulf Coastal Plains fishes that barely impinge upon the Low Plateau in Kentucky without actually penetrating its drainages (Sisk 1973; Baker 1939; Burr and Mayden 1979).

As stated previously, in Kentucky the Land Between the Lakes region (Lower Tennessee-Lower Cumberland rivers) separates the Low Plateau from the Gulf Coastal Plains. The mix of fishes in this area reflects the various centers of origin; some examples are presented in Table 2 (McDonough 1974; Resh et al. 1972). A similar picture is presented by a partial list of fishes from Reelfoot Lake (Table 3), which barely laps northward into Kentucky (Parker 1939; Baker 1939). Some of the fishes in this area and elsewhere in the Low Plateau gained access to the region from the north, possibly via a temporary post-Wisconsin connection between the Erie and Wabash drainages, and Indiana's White and Big Blue drainages (Gerking 1945). They include *Umbra limi* (Kirtland), *Rhinichthys atratulus* (Hermann), *Percopsis omiscomaycus* (Walbaum), and *Fundulus catenatus* (Storer). Jordan (1877) reported

Table 1. Fishes shared by the Tennessee and Alabama River systems (Lee et al. 1980; Smith-Vaniz 1968).

Ichthyomyzon castaneus	*Ictiobus bubalus*
Ichthyomyzon gagei	*Ictiobus cyprinellus*
Lampetra aepyptera	*Minytrema melanops*
Amia calva	*Moxostoma carinatum*
Acipenser fulvescens	*Moxostoma duquesnei*
Scaphirhynchus platorhynchus	*Moxostoma erythrurum*
Polyodon spathula	*Moxostoma macrolepidotum*
Lepisosteus oculatus	*Ictalurus furcatus*
Lepisosteus osseus	*Ictalurus melas*
Anguilla rostrata	*Ictalurus natalis*
Alosa chrysochloris	*Ictalurus nebulosus*
Alosa alabamae	*Ictalurus punctulatus*
Dorosoma cepedianum	*Noturus gyrinus*
Hiodon tergisus	*Pylodictis olivaris*
Esox americanus	*Fundulus olivaceus*
Esox niger	*Gambusia affinis*
Campostoma anomalum	*Labidesthes sicculus*
Hybognathus hayi	*Morone chrysops*
Hybognathus nuchalis	*Morone mississippensis*
Hybopsis storeriana	*Ambloplites rupestris*
Nocomis leptocephalus	*Lepomis cyanellus*
Nocomis micropogon	*Lepomis gulosus*
Notemigonus crysoleucas	*Lepomis humilis*
Notropis atherinoides	*Lepomis macrochirus*
Notropis baileyi	*Lepomis megalotis*
Notropis bellus	*Lepomis microlophus*
Notropis chrysocephalus	*Micropterus punctulatus*
Notropis lirus	*Micropterus salmoides*
Notropis venustus	*Pomoxis annularis*
Notropis volucellus	*Pomoxis nigromaculatus*
Notropis whipplei	*Stizostedion vitreum*
Opsopoeodus emiliae	*Percina caprodes*
Pimephales notatus	*Percina maculatum*
Pimephales vigilax	*Percina ouachitae*
Rhinichthys atratulus	*Percina shumardi*
Semotilus atromaculatus	*Etheostoma nigrum*
Carpiodes cyprinus	*Etheostoma stigmaeum*
Cycleptus elongatus	*Cottus carolinae*
Erimyzon oblongus	*Aplodinotus grunniens*

Etheostoma camurum (Cope), *E. variatum* Kirtland, *E. spectabile* (Agassiz), *Ammocrypta pellucida* (Putnam), and *Percina copelandi* (Jordan) from the White River in Indiana, as well as the minnows *Hybopsis dissimilis* (Kirtland) and *Notropis ariommus* (Cope), and the sucker *Erimyzon oblongus* (Mitchill), most of these doubtless re-invading during post-glacial times via the Ohio River. The Wabash River, however, has been the principal Low Plateau pathway of piscine re-invasion into Indiana and Illinois (Table 4).

At least one species in this area, *Clinostomus funduloides* Girard, reported from the Lower Tennessee (Miller 1978), Cumberland (Burr 1980), and Little Sandy rivers and several other streams in northeast Kentucky (Bauer and Branson 1979), the Wabash drainage in Indiana (Lee et al. 1980; Gerking 1945; Blatchley 1938), and the Barren and Green rivers (Retzer et al. 1983), has a strongly pre-glacial relict distribution. This may be true also of *Rhinichthys atratulus*.

Fishes considered by Etnier (unpublished) to have strong lowland and Lower Mississippi affinities are presented in Table 5. In addition, he believes that several species of Low Plateau fishes are derivable from areas west of the Mississippi, from the Ozarkian and Great Plains faunal regions: *Hybopsis gracilis* (Richardson), *H. storeriana* (Kirtland), *Hybognathus hayi* Jordan, *H. nuchalis* Agassiz, *H. placitus* Girard, *Notropis lutrensis* (Baird and Girard), *N. camurus* (Jordan and Meek), *N. umbratilis* (Girard), *N. fumeus* Evermann, and *N. stramineus* (Cope). Such faunal exchanges could have occurred either via the aforementioned isthmus across southern Illinois and Indiana, or via the Mississippi-Ohio system. To this list should be added the percid subgenus *Nothonotus* (Zorach 1972; Harker et al. 1980) (see discussion below).

Although many fish species enjoy wide distribution throughout the Low Plateau, many others are restricted to certain portions of the area. One of the most interesting of such patterned distributions is endemicity, important in biogeographic studies and presenting several implications. Applied specifically to the Interior Low Plateau aquatic problem, endemicity may reflect interrupted gene flow imposed by isolation resulting from drainage modification and control (cut off from surrounding drainages) by master rivers like the Green (Kuehne 1966) and extralimital origins, dispersal into other drainages and modification and divergence in the new system. For example, Zorach (1972) proposed that the ancestral stock of *Nothonotus* arose west of the Mississippi in the Arkansas or Red River systems and dispersed from there into the Ohio and Tennessee systems, where evolutionary divergence occurred. The Tennessee and Middle Cumberland, and the Green-Barren rivers, seem to have been of great importance as speciation centers. Three dif-

Table 2. Some Land Between the Lakes fishes of Kentucky (from McDonough 1974, and Resh et al. 1972).

Ichthyomyzon bdellium	*Minytrema melanops*
*Lepisosteus oculatus**	*Ictalurus furcatus*
Lepisosteus osseus	*Ictalurus melas*
Lepisosteus platostomus	*Ictalurus natalis*
*Amia calva**	*Ictalurus punctulatus*
Alosa chrysochloris	*Noturus gyrinus*
Hiodon tergisus	*Pylodictis olivaris*
Hybopsis storeriana	*Gambusia affinis*
Nocomis micropogon	*Labidesthes sicculus*
Notropis atherinoides	*Aphredoderus sayanus*
Notropis blennius	*Pomoxis annularis*
Notropis buchanani	*Pomoxis nigromaculatus*
Notropis spilopterus	*Lepomis gulosus*
Notropis whipplei	*Lepomis humilis*
*Opsopoedus emiliae**	*Stizostedion canadense*
Carpiodes carpio	*Stizostedion vitreum*
Carpiodes cyprinus	*Etheostoma asprigene**
Carpiodes velifer	*Etheostoma caeruleum*
Ictiobus bubalus	*Cottus carolinae*
Ictiobus cyprinellus	*Aplodinotus grunniens*
Ictiobus niger	

*Widespread in the Lower Green River portions of the Interior Low Plateau

Table 3. A partial list of fishes from Reelfoot Lake, Tennessee (from Lee et al. 1980, and Parker 1939). Asterisk (*) denotes absence from Low Plateau streams.

Lepisosteus platostomus	*Fundulus notti**
Amia calva	*Fundulus olivaceus*
Alosa alabamae	*Menidia beryllina (audens)**
Hiodon tergisus	*Elassoma zonatum*
Hybognathus nuchalis	*Centrarchus macropterus*
Opsopoedus emiliae	*Lepomis humilis*
Rhinichthys atratulus	*Lepomis symmetricus**
Erimyzon oblongus	*Etheostoma fusiformis**
Noturus gyrinus	*Etheostoma gracilis*
*Umbra limi**	*Etheostoma proeliare*
*Fundulus chrysotus**	

ferent subgenera of darters — four if we accept *Nanostoma* (Page and Burr) — (Table 6), perhaps resulting from various impulses or cycles of invasion from extra-limital stream basins, have markedly diversified within these river systems, doubtless abetted by the notable niche and habitat variability from stream to stream and within drainages.

Actually, the Low Plateau endemic species of the percid subgenera *Nothonotus*, *Catonotus* and *Ulocentra* (including *Nanostoma*) and their nearly 30 species, pose a biogeographic and evolutionary problem of considerable importance that has been inadequately studied. These three groups, in my estimation, are species swarms that have developed in response to mechanisms similar to those proposed by Pflieger (1971) to account for stepwise fish dispersal through the Mississippi and Ohio rivers: "Aggradation subsequent to the last glacial stage produced the environmental conditions now prevailing in the Embayment, restricting further dispersal by upland fishes. All the glacial and interglacial periods were accompanied by alternate entrenchment and aggradation in the Mississippi Embayment, and this would seem to provide an adequate mechanism for the alternate dispersal and isolation of populations east and west of the Embayment."

Thus, this mechanism may have been accompanied by cycles of isolation, adaptation, and speciation, aided by extralimital stream captures that brought congeners back into contact to heighten competition and perhaps establish new patterns of variation and divergence. Whatever the mechanisms and processes, the species swarms are real and the whole problem is deserving of detailed analysis.

Another group of fishes of considerable interest and importance is the ictalurid genus *Noturus*. The fact that most species of *Noturus* avoid cold water (Taylor 1969) indicates a southern origin for the group. The center of greatest abundance of species encompasses Kentucky and Tennessee to Virginia and North Carolina, with a derivative secondary speciation center in the Ozarks of Arkansas and Missouri. Tennessee has the largest number of species, mostly associated with the Tennessee River basin, Kentucky is second followed by Alabama, and the number decreases peripherally. *Noturus gyrinus* (Mitchill), a distinctive lowland species that is widespread and common in the Lower Green and Tradewater systems, gets into Low Plateau streams in western Kentucky and adjacent Indiana and Illinois (Wabash drainage). *Noturus exilis* Nelson is absent from southern Indiana and most of Kentucky, but occurs in extreme southwestern Illinois, much of the Low Plateau of central Tennessee and northern Alabama, and peripheral areas to the north (postglacial) and trans-Mississippian in Oklahoma, Kansas, Missouri, and Arkansas. In the Low Plateau, *Noturus nocturnus* Jordan and Gilbert occurs in the Tennessee River drainage of western Tennessee, northern

Table 4. Wabash River fishes in Indiana derived from Mississippi Embayment and Low Plateau sources (from Gerking 1945, and Blatchley 1938).

Polyodon spathula	*Gambusia affinis*
Lepisosteus oculatus	*Morone mississippiensis*
Lepisosteus spatula	*Centrarchus macropterus*
Alosa chrysochloris	*Lepomis humilis*
Hiodon alosoides	*Ammocrypta clara*
Clinostomus elongatus	*Etheostoma asprigene*
Hybopsis aestivalis	*Etheostoma chlorosomum*
Hybopsis storeriana	*Etheostoma gracile*
Hybognathus hayi	*Etheostoma histrio*
Hybognathus nuchalis	*Etheostoma squamiceps*
Notropis buchanani	*Etheostoma variatum*
Carpiodes carpio	*Percina copelandi*
Carpiodes velifer	*Percina evides*
Cycleptus elongatus	*Percina ouachitae*
Moxostoma carinatum	*Percina sciera*
Moxostoma macrolepidotum	*Percina shumardi*
Noturus nocturnus	

Table 5. Fishes of the Low Plateau derived from lowland and lower Mississippi sources (from Etnier, unpublished).

Notropis buchanani	*Etheostoma chlorosomum*
Notropis maculatus[1]	*Etheostoma gracile*
Notropis shumardi	*Etheostoma histrio*
Notropis venustus	*Etheostoma parvipinne*
Opsopoedus emiliae	*Etheostoma spectabile*[3]
Phenacobius mirabilis[2]	*Etheostoma swaini*
Erimyzon succetta	*Percina evides*[2]
Moxostoma poecilurum[1]	*Percina phoxocephala*
Noturus phaeus[1]	*Percina sciera*
Noturus stigmosus	*Percina shumardi*
Etheostoma asprigene	

[1]Not in Low Plateau
[2]Plains origin
[3]Trans-Mississippian origin

Alabama, and Western Kentucky, from whence it has been able to extend its range up the Ohio into the Wabash River drainage of Illinois and Indiana, the Green River of Kentucky, and old Teays tributaries (Kentucky and Big Sandy rivers) in eastern Kentucky. *Noturus phaeus* Taylor and *N. hildebrandi* (Bailey and Taylor) have ranges that only impinge upon the Low Plateau in Mississippi River drainages of northern Alabama and western Tennessee, *N. phaeus* barely getting into southwestern Kentucky (Terrapin Creek) (Taylor 1979). *Noturus flavus*, being more tolerant of cold water, is distributed throughout much of the upper two-thirds of the Mississippi drainage, including most of the Low Plateau. *Noturus elegans* Taylor, autochthonous to the Barren-Green system of Kentucky and adjacent Tennessee, has an apparently disjunct population in the Tennessee River basin (Duck River). In the Low Plateau, *N. eleutherus* occurs in the Tennessee (no published records from Kentucky stretches of that stream), the Green River, and the Wabash system of Illinois and Indiana. *Noturus stigmosus*, a member of the *furiosus* species complex, avoids most of the Low Plateau but has penetrated into the Green and Salt river drainages of Kentucky and into the Wabash River of Illinois-Indiana. *Noturus miurus* has the widest distribution of all Low Plateau madtoms, having been reported from all drainages.

It seems likely that the ancestral stock of *Noturus* arose somewhere in the lowlands of the Mississippi River basin from a bullhead-like ancestor (Taylor 1969), and spread from there into other parts of America. Using the Tennessee River basin as a speciation center, additional species diverged and spread widely throughout the system in pre- and postglacial times, particularly after development of the Upper Ohio system. Such conclusions are supported by the paucity of *Noturus* species in the Eastern Seaboard drainages.

The occurrence of *Moxostoma* (*Thoburnia*) *atrippine* Bailey — a close relative of the torrent suckers of Virginia — in the Barren River system of the Low Plateau either represents a relict or a case of immigration, extinction in intervening areas, and survival and divergence. The wide hiatus in ranges between population centers in the subgenus *Thoburnia* suggest the latter.

CONCLUSIONS

The examples of Interior Low Plateau aquatic biota discussed here merely represent the complexity of the mechanics and biologistics of understanding such a fauna and flora. I have not discussed other taxa, such as the swarms of unionid pelecypods and decapod crustaceans, because that would have lengthened the paper considerably. However, the distributional patterns of these interesting organisms also very graphically reflect similar conclusions.

Table 6. Endemic fish species of various streams of the Interior Low Plateau and vicinity.

Species	River System	Literature Source
Nothonotus		
Etheostoma bellum	Green	Zorach 1968
Etheostoma chlorobranchium	Tennessee	Zorach 1972
Etheostoma microlepidum	Lower Cumberland	Raney and Zorach 1967
Etheostoma aquali	Duck, Buffalo	Williams and Etnier 1978
Catonotus		
Etheostoma virgatum	Cumberland	Kuehne and Small 1971
Etheostoma obeyense	Upper Cumberland	Kuehne and Small 1971
Etheostoma barbouri	Barren and Green	Kuehne and Small 1971
Etheostoma luteovinctum	Duck and Cumberland	Lee et al. 1980
Etheostoma smithi	Lower Cumberland, Tennessee	Page and Braasch 1976
Etheostoma striatulum	Duck	Page and Braasch 1977
Etheostoma oilvaceum	Caney Fork	Braasch and Page 1979
Etheostoma neopterum	Tennessee	Howell and Dingerkus 1978
Etheostoma species	Tennessee	Howell and Dingerkus 1978
Etheostoma species	Tennessee	Howell and Dingerkus 1978
Etheostoma obeyense	Cumberland	Clay 1975
Ulocentra		
Etheostoma etnieri	Caney Fork	Lee et al. 1980
Etheostoma barrenense	Barren	Page and Burr 1982
Etheostoma rafinesquei	Upper Green, Lower Barren	Page and Burr 1982
Etheostoma simoterum[1]	Tennessee	Lee et al. 1980
Etheostoma atripinne[1]		
Etheostoma species	Obion and Forked Deer	Lee et al. 1980
Etheostoma coosae	Conasauga	Lee et al. 1980
Etheostoma species	Middle Tennessee	Lee et al. 1980
Etheostoma species	Conasauga	Etnier, unpublished
Etheostoma duryi	Tennessee	Lee et al. 1980
Etheostoma species	Lower Green	Burr 1980
Etheostoma species	Blood, Clarks	Burr 1980
Allohistium		
Etheostoma cinereum[2]	Tennessee, Cumberland	Lee et al. 1980
Oligocephalus		
Etheostoma boschungi	Tennessee	Wall and Williams 1974
Catostomidae		
Moxostoma atripinne	Green and Barren	Kuehne and Small 1971
Cyprinidae		
Nocomis effusus	Cumberland, Green, Lower Tennessee	Lachner and Jenkins 1967

[1]Probably conspecific

[2]Principally a Low Plateau species but known from Ridge and Valley Province

The Interior Low Plateau is a unique province in many ways. The region has been periodically convulsed by tectonic readjustments of the crust that stimulated some reorganization of drainages. It was also influenced by the formation and maintenance of the Mississippi Embayment and the isthmus of stable land at the northwest corner of the Low Plateau, and/or by eustatic adjustments of the Embayment, and by stream evolution and modification in extralimital areas, mostly taking the form of headwater piracies between various streams. Pleistocene glaciation caused enormous changes by obliterating much of the old Teays River system and other streams in the unglaciated area, and by successively turning streams westward to form the Upper Ohio River, connecting streams that had never before been in direct contact. This, and the placement of the Mississippi Embayment, conspired to form one of the most unusual hydrologic phenomena in North America. More large rivers find confluence near the junction of Illinois, Indiana, Missouri, and Kentucky than at any other area of equal size in North America: the Ohio, Mississippi, Tennessee, Cumberland, Green, and Wabash rivers. Some of these streams run in nearly ancestral basins, but others do not. The biological function of all these changes was, of course, to open up faunal exchange pathways that had not previously been available. The influence of the Mississippi-Ohio connection upon the repopulation of Indiana and Illinois segments of the Wabash drainage has been very great. During meltback, many small streams were doubtless exterminated and larger ones modified by outwash and deposition, judging from the thickness of known deposits in Indiana and adjacent Kentucky and the fossils contained therein.

Stream-margin and tributary migration ("hopping"), both upstream and downstream, is still a viable hypothesis to explain some observed distributional patterns in small-stream (third order and smaller) species. The meltback of even enormous glaciers is not a constant phenomenon, but one that varies according to season and even time of day, creating impulses of high- and slack-water conditions. Where warmer water flows into glacial streams, the warm water does not mix immediately with the cold. Instead, as I have observed at the Athabascan Ice Field in Canada and at many smaller valley glaciers in British Columbia, Washington, and Oregon, the warmer water flows along the margins of the current. Thus, in the case of Interior Low Plateau drainages, various species of fishes could have found their way into tributaries where they had not previously occurred.

There were, of course, fishes already present in Low Plateau streams prior to the onset of these influences; some of those remain as relicts, either as endemics or as segments of the fauna that are identical with or closely related to segments elsewhere with varying hiatuses intervening. Newly arrived forms from elsewhere may have, because of narrow habitat or niche requirements, remained close to the points of entry (as in the case of some of the headwater species), or they may have spread inexorably through systems, progressively coming into competition with members of the preexisting fauna. Such competition may have caused some minor extinctions here and there by way of niche replacement, but it probably stimulated subdivision of niches and, apparently, considerable sequences of divergence, speciation, and other types of faunal readjustments. Some speciation may have been stimulated by the presence of unoccupied niches, by the habitat fluctuations associated with long-term geologic influences, and by differences between various segments of Low Plateau drainages.

All these influences have acted in concert to create a superior aquatic fauna in the streams and rivers of the Interior Low Plateau, but one which has remained relatively poorly understood until recent times, particularly in its relationships to extralimital drainages. Now a new factor has been superimposed upon natural ones, a factor that not only threatens the integrity of the fauna and flora (Branson 1977), but one that also threatens our ability to understand this biota. The results of preimpoundment studies indicate that some species, present prior to damming of streams, are now either very rare or unknown from afflicted areas. An example is *Hybognathus nuchalis* (pers. comm., David Etnier and students, following study of University of Michigan holdings). Every major stream that flows through the Low Plateau bears dams, sometimes multiple ones. These structures have vastly modified habitats, upset temperature regimens, and diminished nutrient flow through the systems. Exotic species and transplanted ones, such as striped bass, trout, and threadfin shad, have gotten into the system, creating stress that was not earlier present. Previously autonomous drainages are now interconnected. For example, a navigation canal joins the Cumberland and Tennessee rivers at Land Between the Lakes; other connections are planned, such as the Tennessee-Tombigbee Waterway. Coal mining and channelization continue to inflict adverse changes in many Low Plateau streams. Other recent influences are steadfastly afflicting this unique fauna, bringing many species to levels of concern (Branson et al. 1981). Most are associated with human population pressures, the changing financial picture, and the energy crisis. Hopefully, we have learned enough to preserve at least the principal genomes of the Low Plateau biota.

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